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BOTANICAL GAZETTE

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ON THE ORIGIN OF THE BROAD RAY IN QUERCUS

CONTRIBUTION FROM THE PHANEROGAMIC LABORATORY OF HARVARD UNIVERSITY NO. 17

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(WITH PLATES VIII AND IX)

As is shown in KNY'S *Botanische Wandtafeln*, nos. 75 and 76, the wood of Quercus consists of vessels, tracheids, fibers, and parenchyma. The last is disposed in two systems: the vertical, consisting of more or less scattered rows of cells, forming the xylem parenchyma; and the horizontal, made up of plates of cells extending radially, the medullary rays. The latter are of two sorts: small, numerous rays, which are thin sheets of tissue, linear, and of a single row of cells as seen in transverse and tangential sections; and occasional broad, generally fusiform masses, many cells wide, which form the most prominent feature of oak wood, its remarkable "silver grain." In our first two figures both kinds of rays are seen: *fig. 1* shows in transverse section a portion of a large ray, and of several small ones from the wood of *Quercus rubra;* and *fig. 2*, the tangential view of similar rays in the same species.

In the study of sections of a fossil oak from the gold gravels of California (Miocene), the material for which was kindly loaned the Phanerogamic Laboratories of Harvard University for investigation, an unusual ray structure was noticed. The uniseriate rays are present as in the living oaks; the large rays, however, are not homogeneous masses of parenchyma, but are represented by groups of smaller rays. *Fig. 6* shows such a group in tangential view. The smaller rays are so arranged as to form, in aggregate, the elongate fusiform mass of the normal large ray. They are separated from each other, however, by fibers, or by fibers and wood parenchyma.

A portion of the cluster more highly magnified is shown in *fig. 10*. *Fig. 5* shows the appearance of this "false" ray in transverse section.

This structure led to the suspicion that the large rays of the existent oaks might be derived from the so-called "false rays" of the lower Cupuliferae; that is, that the former have been "built up" by the aggregation and fusion of the small rays. The Miocene fossil would then represent a comparatively recent ancestral condition in ray structure. Two American species of Quercinium from Tertiary deposits in the Yellowstone National Park, *Quercinium Knowltonii* Felix[1] and *Q. lamarense* Knowlton,[2] have rays which seem, from the figures and descriptions, to be very much like those of the fossil here figured. The question then arose whether the seedlings of our living species of Quercus do not present some evidence as to the origin of the larger rays in living oaks, inasmuch as the seedling is known to be a seat of ancestral characters. The investigation of a number of North American species showed that we have in the oaks a good example of seedling recapitulation.

The oaks, from paleobotanical evidence, seem to have descended from ancestors that resembled the living chestnuts. There is much similarity in the structure of the reproductive organs, and in the type of leaf shape of the oldest oaks, and of the chestnuts. Confirmatory evidence is presented by the seedlings of some of our living oaks; especially worthy of notice is the fact that the first rays formed are all of the type which is found throughout chestnut wood.

In respect to ray structure in the seedlings, the species examined fall into two groups, corresponding with the subgenera Lepidobalanus (white oaks), and Erythrobalanus (red or black oaks).

The seedlings of the black oaks that were examined by the writer (*Q. rubra* L., *Q. velutina* Lam., *Q. coccinea* Moench., and *Q. ilicifolia* Wang.) all show a ray structure very much like that of the gold gravel oak above described. In the early annual rings, from the first or third to about the fifteenth, a progressive compounding, that is grouping and fusion, of the linear rays occurs, with the final production, after the considerable period of compounding, of a single, huge, homogeneous ray. *Fig. 3* shows this process in a seedling of *Q. velutina*, the partial formation of three rays being evident. The ultimate shape and structure is brought about by the loss of the separating rows of fibers, tracheids, or wood parenchyma, or rather by the transformation of the elements included by the rays as they approach one another. This change is gradual; more and more parenchyma is formed, with corresponding decrease in fibers, until the cambial cells that lay down these radial rows cut off only ray cells. Ray formation of this sort exists in these species only as a passing phase in the seedling. In the wood of the mature plants large rays, of course, are continually formed, but their origin is nearly always abrupt. The transition from lignified elements to parenchyma occurs generally within the width of a single annual ring, or sometimes two or three. Later there is usually an increase in width which is due, however, not to the uniting of any neighboring small rays and the transformation of adjacent elements, but to simple growth in size with the increase of the stem in diameter. The seedlings of the black oaks, then, give evidence of the mode of origin of the broad rays so characteristic of the mature wood of the group. In so doing they repeat the ray structure that probably occurred throughout the wood of their rather recent ancestors.

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[1] FELIX, J., Untersuchung über fossile Hölzer. Zeit. Deutsch. Geol. Gesells. —:250. *pl. 6.* 1896.

[2] KNOWLTON, F. H., Geology of the Yellowstone National Park. Part II. U. S. Geol. Survey. p. 771. *pls. 118, 120, 121.* 1899.

Among the white oaks, seedlings of *Q. alba* L., *Q. bicolor* Willd., and *Q. prinoides* Willd. were examined. In all three species the wood of the stem for a distance of several inches, or even one or two feet, above the root possesses only uniseriate rays. Moreover, until the plant has attained a considerable size no large rays nor any signs of grouping of the small rays appear. Cases were seen in *Q. alba* and *Q. bicolor*, where in seedlings 15 to 20 years old only the linear rays existed. This condition would suggest that these white oaks, perhaps, are somewhat more primitive than the black oaks, for the seedlings of the former revert in structure to an ancestral type in which only uniseriate rays existed, and had not as yet begun to aggregate. *Fig. 7* shows a transverse view of this condition in *Q. alba* in about the fifteenth to twentieth annual rings. When the large rays do appear in these species, they are formed as in the black oaks, rather abruptly, the phase of compounding being confined to only one or two annual rings. Often nearly the whole ray arises at once at the beginning of a season's growth; a continuous row of cambial cells which have hitherto laid down chiefly fibers and tracheids, beginning with the first divisions of the year, form ray cells and only such thereafter. This is also the method in the stem of the mature plant.

Among the living oaks there are exceptions, however, to the possession of rays of the type shown in *figs. 1* and *2*. *Q. virginiana* Mill. (*Q. virens* Ait.), the live oak, has large rays of a type in which the compounding has become nearly complete. This species is probably somewhat more primitive than the above-mentioned species. *Fig. 8* shows a tangential section of a ray from near the pith in a large seedling of this plant. The structure of this ray very much resembles that of the fossil oak and of the black oak seedlings. In *fig. 9* a portion of this ray is shown enlarged. The Japanese oaks have somewhat similar structure of the broad medullary rays, *Q. Mirbeckii* and *Q. Sieboldii* especially. In the shape of their leaves the oaks of Japan show other probable signs of primitiveness; the general type is similar to that of the chestnuts.

Not only does the large ray in its primitive condition occur in fossil and seedling oaks, and occasionally in mature plants of the genus, but it exists also in several genera of the lower Cupuliferae, namely in Corylus, Carpinus, Ostrya, Betula, Alnus, and perhaps others. The distribution of the large rays in the dicotyledons is at present being investigated in this laboratory by Mr. I. W. BAILEY. *Figs. 11* and *12*, transverse and tangential sections, respectively, of the wood of *Alnus incana* (L.) Moench., show in one of these genera this "false ray." In this case the linear rays have become grouped together, but very little fusion has yet taken place. It would seem then that this fusion of rays, perhaps for the acquisition of greater storage capacity, which began in some primitive cupuliferous plants, and which is still maintained at an early stage in some of the living members thereof, has reached a culmination in the broad, solidly parenchymatous mass, the large ray, of many living oaks.

That the "false ray" of Alnus and of other closely allied genera represents the primitive condition of the present large ray of Quercus seems undoubted, not only from its appearance in the lower Cupuliferae, and in fossil and seedling oaks, but also from many other points of resemblance. A prominent feature of the broad ray of Quercus is the strong "dipping in" of the annual ring wherever these radial masses of parenchyma occur. This is well shown in *fig. 1*. In the cases among the lower Cupuliferae, and in fossil species of Quercus where rays of the compound type exist, the same feature is noticeable. In Alnus, as appears in *fig. 11*, this condition is prominent; in the fossil oak it can be seen, but only faintly, for the annual rings are not strongly marked, probably as a result of the milder climate of the Miocene. This peculiarity serves thus further to connect the two kinds of rays.

In view, then, of the apparent phylogenetic relation of the two sorts of medullary rays found in Quercus, the designation of the broad ray as *primary* and of the small one as *secondary*, a use that is to some extent prevalent, seems inadmissible. The terms would certainly be more applicable if interchanged, but the adjectives *small* and *broad* or *large*, or *small* and *compounded* may perhaps be more appropriately applied.

Summary

The medullary rays of the oak are of two sorts: small, linear sheets of parenchyma, only a single row of cells wide, as seen in transverse and tangential sections; and large, generally fusiform masses, many cells in width. The former have been to some extent called secondary rays, the latter primary rays.

Fossil evidence points to the probable derivation of the existent oaks from ancestors which possessed only the linear type of ray. The large ray has apparently originated by the aggregation and fusion of many of these small rays, through the loss of the separating elements, or the transformation of the latter into ray cells. A fossil oak from the Miocene gold gravels of California shows an intermediate condition, a stage where all the large rays consist merely of aggregations of small rays, with separating fibers. The seedlings of some, at least, of the black oaks form rays of this nature for a brief period, usually during the first ten to fifteen years. There is during this time a recapitulation of the history of the development of the ray; the small, uniseriate rays, which are at first formed, gradually approach each other in groups, and fusion slowly occurs as growth of the stems continues, until a good-sized, homogeneous, parenchymatous ray is formed. In the wood of the mature plant the large ray is formed more abruptly, and is not so much the result of fusion of smaller rays, as of the transformation of all tissue, within a region of the size of the ray to be formed, into ray parenchyma, such change being rather abrupt and occurring largely at the beginning of a season's growth. The seedlings of the white oaks possess in their early wood only uniseriate rays, suggesting a somewhat more primitive state. A few living oaks show the transitional stage, that is, large rays composed of ununited aggregations of small rays in the wood of mature plants. The Japanese oaks especially belong in this group.

The oaks present an excellent case of recapitulation of ancestral characters by seedlings. The phylogenetic history of ray structure in the genus is well displayed, step by step, in the wood of the seedling stem during the first few years.

The work has been carried on in the Phanerogamic Laboratories of Harvard University. The writer desires to express his thanks to Dr. F. H. KNOWLTON of the United States Geological Survey for the loan of material of miocene oaks, and to Mr. I. W. BAILEY for opportunity to examine and use slides of several genera of cupuliferous woods. He is also very much indebted to Professor E. C. JEFFREY for suggestions and advice during the progress of the investigation.

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EXPLANATION OF PLATES VIII AND IX

PLATE VIII

FIG. 1.—*Quercus rubra;* transverse section of wood, showing portions of large and small medullary rays. ×40.

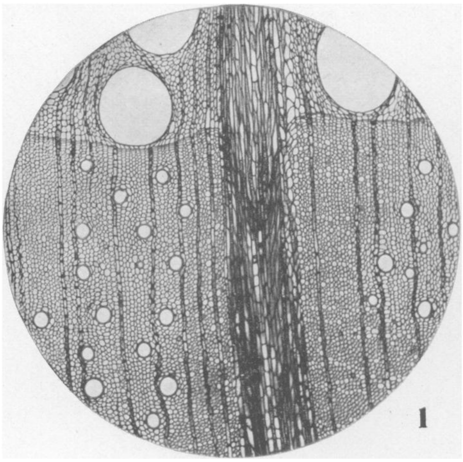
FIG. 2.—The same; tangential section of wood, showing similar rays. ×40.

FIG. 3.—*Quercus velutina*, seedling; transverse section of portion of stem showing formation of large rays. ×40.

FIG. 4.—*Quercus rubra*, seedling; tangential section of a large ray in process of formation. ×40.

FIG. 5.—Fossil oak from gold gravels of California (Miocene); transverse section of wood showing portion of the large ray. ×40.

FIG. 6.—The same; tangential view of portion of the large ray. ×40.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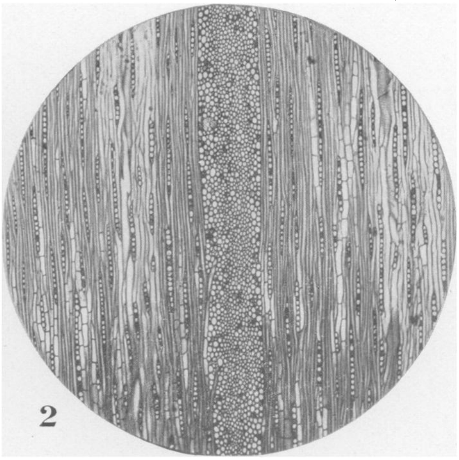
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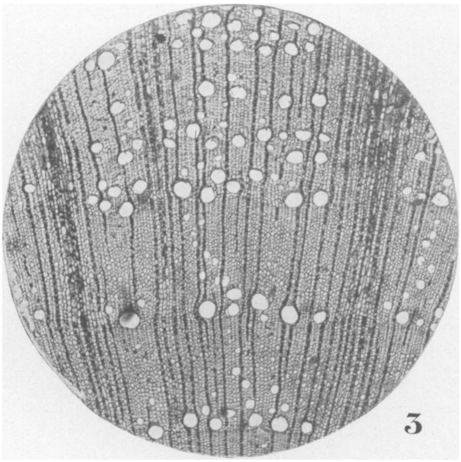
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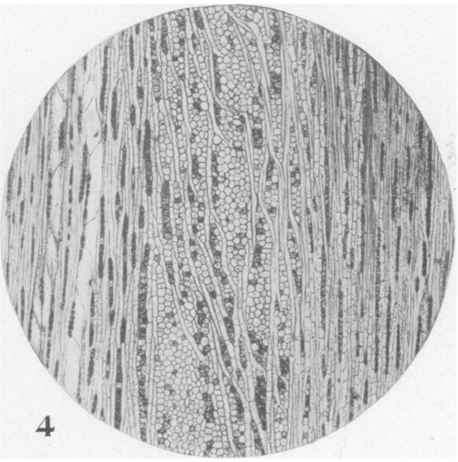
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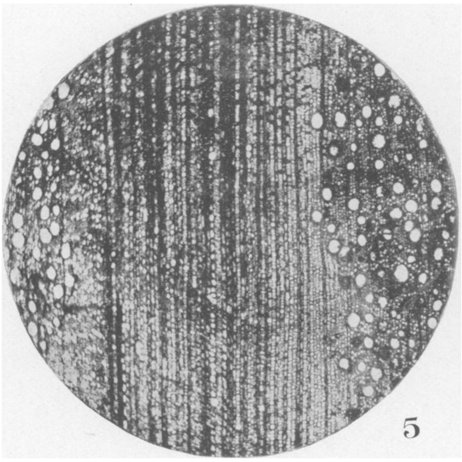
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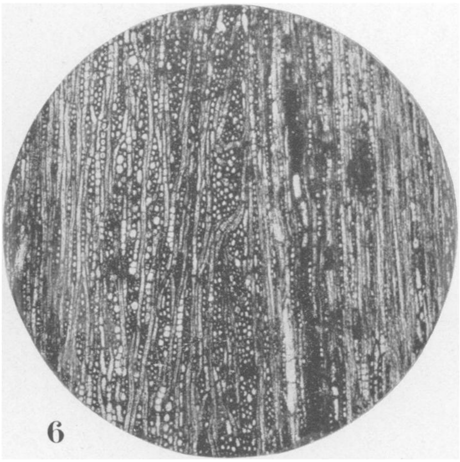
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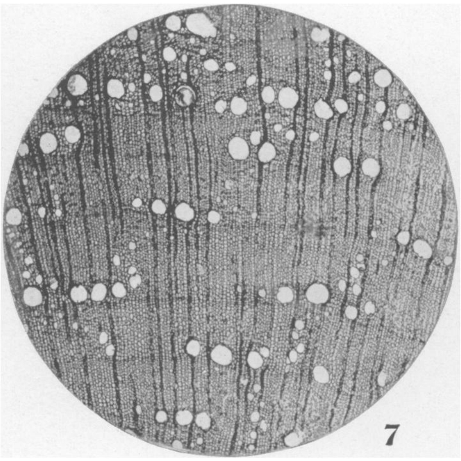
EAMES on QUERCUS



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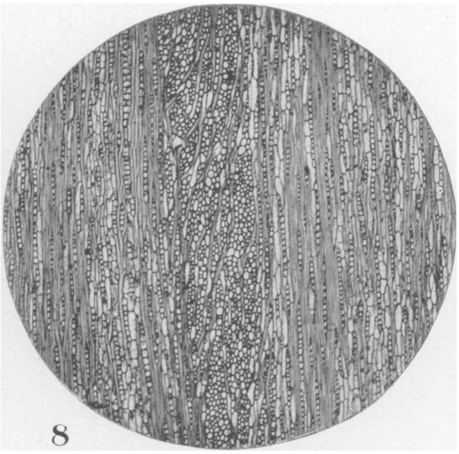

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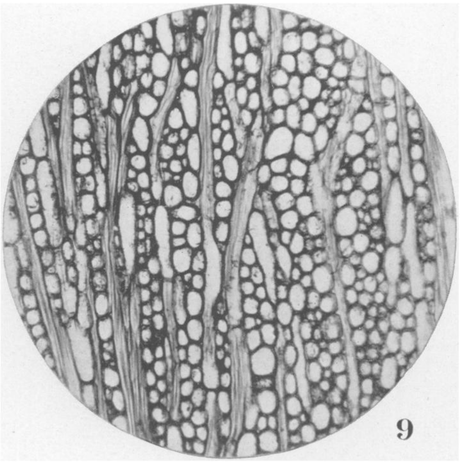

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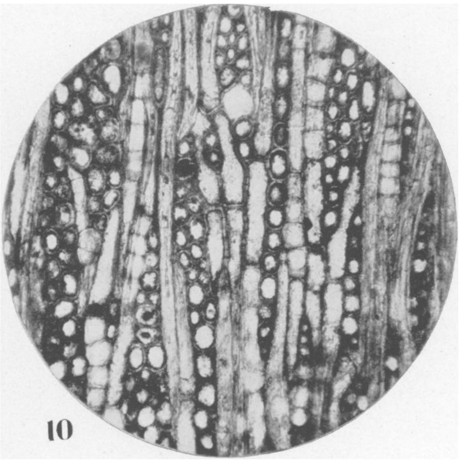

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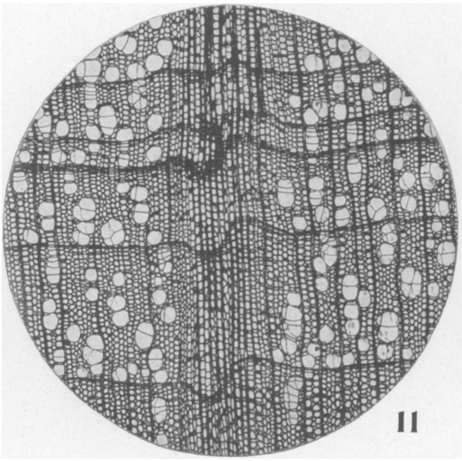

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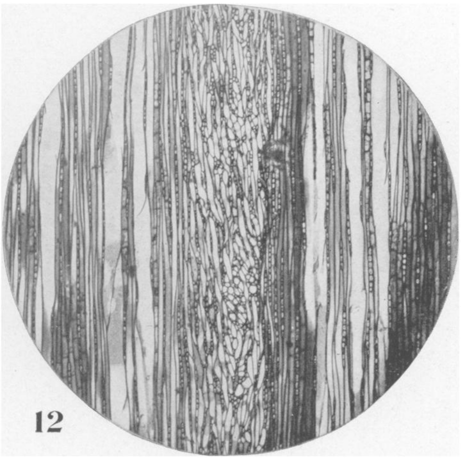

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EAMES on QUERCUS

PLATE IX

FIG. 7.—*Quercus alba*, seedling; transverse section of portion of stem, showing only rays of the linear type. ×40.

FIG. 8.—*Quercus virginiana*, seedling; tangential view of portion of large ray. ×40.

FIG. 9.—The same; portion of the large ray. ×100.

FIG. 10.—Fossil oak of the gold gravels; tangential view of portion of the large ray. ×100.

FIG. 11.—*Alnus incana;* transverse section of wood. ×40.

FIG. 12.—The same; tangential section. ×40.